Genetic contribution of three introduced life history forms of sockeye salmon to colonization of Frazer Lake, Alaska

Carl V. Burger, Kim T. Scribner, William J. Spearman, Charles O. Swanton, and Donald E. Campton

Abstract: Colonization of Frazer Lake (Kodiak Island, Alaska) by sockeye salmon (*Oncorhynchus nerka*) represents a rare, successful introduction of this species into a new environment. Eggs, fry, and adults were introduced repeatedly into Frazer Lake from 1951 to 1971. Donors originated from three source populations, each with different life histories: late-run *lake shoreline* spawners (Karluk Lake), early-run *inlet tributary* spawners (Red Lake), and late-run *lake outlet* spawners (Ruth Lake). We used six nuclear DNA (nDNA) microsatellite loci and mitochondrial DNA (mtDNA) to determine which donor population(s) had colonized the principal spawning habitats of Frazer Lake: three shoreline areas and four inlet tributaries. Based on nDNA comparisons, two shoreline-spawning populations were most similar to the shoreline donor, and the four tributary-spawning populations were most similar to the tributary donor. However, five of the seven Frazer Lake populations appeared to be influenced genetically by more than one donor. Genetic distances based on mtDNA were independent of life histories with high (relative to nDNA) interpopulation variation, suggesting significant female founder effects and poststocking drift. Our data suggest that life history adaptations of donor populations were critically important for successful colonization of Frazer Lake, thus underscoring the need to consider life history traits in other introduction and recovery programs.

Résumé : La colonisation du lac Frazer (île Kodiak, Alaska) par le Saumon rouge (*Onchorhynchus nerka*) est une des rares introductions réussies de cette espèce à un nouveau milieu. Des oeufs, des alevins et des adultes ont été introduits à plusieurs reprises de 1951 à 1971. Les donneurs provenaient de trois populations-souches, chacune possédant une démographie particulière: des poissons à montaison tardive qui fraient près des rives du lac (lac Karluk), des poissons à montaison précoce qui fraient dans les tributaires (lac Red) et des poissons à montaison tardive qui fraient dans l'émissaire (lac Ruth). L'étude de six locus microsatellites d'ADN nucléaire (ADNn) et d'ADN mitochondrial (ADNmt) a permis de déterminer quelles populations-souches avaient colonisé les principales frayères du lac Frazer, trois zones de rivage et quatre tributaires. D'après la comparaison des ADNn, deux les populations des frayères de rivage étaient plus semblables au donneur frayant sur les rives et quatre des populations des frayères dans les tributaires ressemblaient plus au donneur frayant dans les tributaires. Cependant, cinq des sept populations du lac Frazer semblaient être affectées génétiquement par plus d'un donneur. Les distances génétiques basées sur l'ADNmt étaient indépendantes des caractéristiques démographiques et elles affichaient une forte variabilité (par comparaison à l'ADNn) d'une population à l'autre, ce qui suggère d'importants effets du fondateur femelle et une dérive après l'empoissonnement. Ces résultats indiquent que les adaptations démographiques des populations des donneurs ont été des facteurs critiques du succès de la colonisation au lac Frazer, ce qui souligne la nécessité de tenir compte des caractéristiques démographiques lors de programmes de colonisation et de récupération.

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Introduction

Introductions and transplants of salmonid fishes have been extensive during the previous century. A common goal of such programs has been the establishment of self-sustaining, naturally spawning populations to create new fisheries, reverse declines, or enhance harvest opportunities in modified watersheds. Transplants of anadromous and nonanadromous salmonids have often resulted in new, self-sustaining populations in locales where the introduced species was historically absent (Krueger and May 1991; Quinn et al. 1998). However, introductions of anadromous salmonids *within* their native geographic ranges have often been unsuccessful at achieving intended goals (Withler 1982). Reasons underlying introduction failures are not well documented but may be related to biological incompatibilities between the life history adaptations of the donor populations and the geographic, hydrologic, or ecological characteristics of recipient environments (Allendorf and Waples 1996).

Among Pacific salmonids, there have been numerous attempts to introduce sockeye salmon (*Oncorhynchus nerka*) and its nonanadromous life history form (kokanee) into new environments (Withler 1982; Wood 1995). However, in contrast with kokanee, almost all attempts to establish introduced, self-sustaining populations of the anadromous form have failed (Wood 1995). Most introductions of sockeye salmon occurred prior to an understanding of the genetically based life history and ecological adaptations of anadromous populations. As a result, introduced sockeye salmon have established self-sustaining populations in only three drainages in western North America: Lake Washington in Washington State, the Upper Adams River in British Columbia, and Frazer Lake on Kodiak Island in Alaska (Wood 1995), all within the species' native range. Introductions into Lake Washington are not well understood because detailed records are lacking, but at least two donor populations are known to have been used, one of which appears to have made detectable genetic contributions to natural populations (see Hendry et al. 1996). Introductions of sockeye salmon into the Upper Adams River (Williams 1987) and into Frazer Lake (Blackett 1979) also involved multiple donor populations, suggesting that a breadth of genetic and phenotypic diversity may be necessary for successful colonization via artificial transplants. However, the relative genetic contributions of multiple donor populations to a single lake–river system, including the factors responsible for successful colonization, are largely unknown.

Sockeye salmon are distinguished from other species of Pacific salmon by the use of lakes as nursery areas for presmolt juveniles prior to seaward outmigration and by the existence of multiple seasonal forms (distinct life history patterns) that frequently co-occur within a single lake–river system. For example, "early-run" adults typically spawn in lake inlet tributaries during summer, whereas "late-run" adults typically spawn along lake shorelines and in outlet rivers during fall (Burgner 1991; Burger et al. 1995). These life history patterns are common throughout the native geographic range of sockeye salmon, which extends from the Snake and Salmon rivers in Idaho to northern Japan and includes most lake–river systems in Alaska, British Columbia, and eastern Russia (Burgner 1991).

Genetic adaptations appear to be closely associated with the life history diversity of sockeye salmon. In both field and laboratory studies, lake outlet spawning adults produce progeny that actively swim upstream against water currents, whereas progeny of inlet tributary spawners passively move downstream, behaviors that appear to be genetically based adaptations for fry to reach nursery lakes (Raleigh 1967; Brannon 1972). Similarly, differences in spawning times and locations between early- and late-run sockeye adults also appear to reflect genetically based life history adaptations (Wilmot and Burger 1985; Burger et al. 1997). Thus, temporal and spatial reproductive adaptations of adults have required corresponding adaptations in juvenile behavior. The specific habitat requirements of different seasonal runs (Varnavskaya et al. 1994), coupled with precise migration and spawning times synchronized with home-stream thermal regimes (Brannon 1987; Burger et al. 1995, 1997), may be additional factors why many introduction efforts have failed to produce self-perpetuating runs of anadromous sockeye salmon. Genetic and phenotypic variation, even over microgeographic scales (e.g., single drainages), can provide insights for matching donor populations with environmental regimes of recipient habitats.

Phylogeographic characterizations based on molecular and biochemical markers have been useful in addressing questions of population structure and ancestral origin of Pacific salmonids. Analytical approaches have relied on protein-coding allozyme loci (Wilmot and Burger 1985; Wood et al. 1994), mitochondrial DNA (mtDNA) (Bickham et al. 1995), or a combination of techniques (Burger et al. 1997; Allendorf and Seeb 2000) to describe population structure. More recently, nuclear DNA (nDNA) markers at microsatellite loci (Scribner et al. 1996, 1998) have been used. Several investigators have addressed ancestral origins of introduced salmonid populations with molecular genetic markers (Hendry et al. 1996; Quinn et al. 1996). Results of such studies often emphasize the importance of temporal and spatial life history attributes as variables affecting the degree of reproductive isolation and, concomitantly, population genetic structure. Effective management of Pacific salmon relies on knowledge of how genetic variation is partitioned within and among populations and of the relative importance of ecological factors to interpopulation levels of genetic variation. Such information may be critical to the success of salmonid reintroduction and restoration strategies.

We describe the genetic contribution of three donor populations to introduced, self-sustaining populations of sockeye salmon in Frazer Lake. Frazer Lake was historically barren of anadromous fishes because of an impassable waterfall in its outlet river. Beginning in 1951 and continuing through 1971, sockeye salmon from three geographically discrete donor populations, each with different life history adaptations, were introduced into Frazer Lake: early-run inlet tributary spawners, late-run lake shoreline spawners, and late-run lake outlet spawners. A fishway was constructed around the outlet waterfall (1962) to let naturally returning adults reenter the lake. We used nDNA markers at six microsatellite loci and mtDNA to compare allele and haplotype frequencies, respectively, of contemporary sockeye salmon spawners in three shoreline areas and four inlet tributaries of Frazer Lake with those of the three donor populations. Our goal was to

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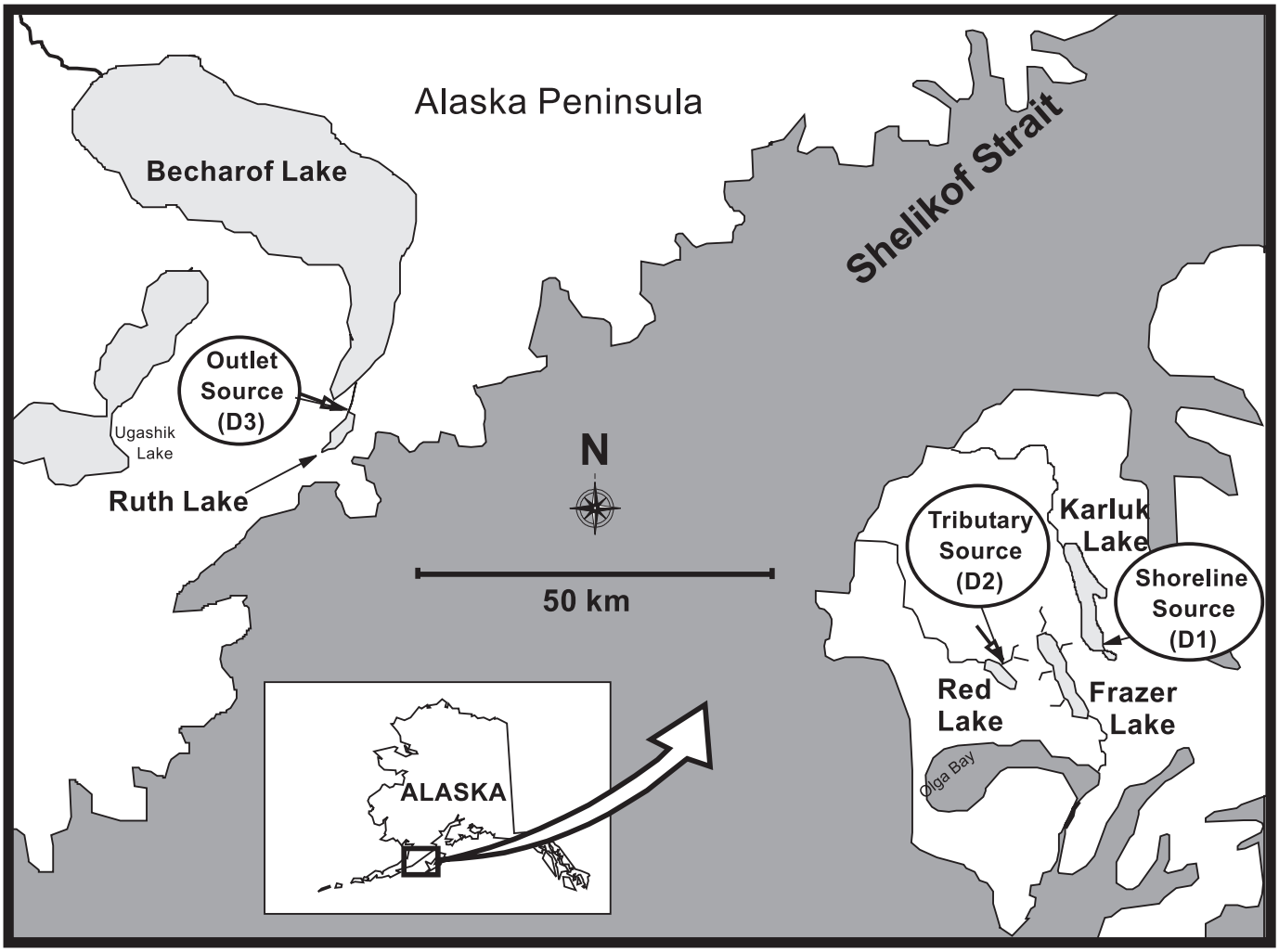
Fig. 1. Geographic locations of three donor populations used to introduce sockeye salmon into Frazer Lake on Kodiak Island, Alaska, 1951–1971. The three donor sources represented a shoreline-spawning population from Karluk Lake (D1), inlet tributary spawners from Red Lake (D2), and a lake outlet spawning population from Ruth Lake (D3).



identify the donor population(s) that contributed genetically to contemporary Frazer Lake production. Also, we wanted to determine whether donors founded recipient populations in Frazer Lake habitats consistent with donor life history type. Our null hypotheses were that (*i*) a single, panmictic population of sockeye salmon currently spawns in the Frazer Lake watershed and (*ii*) the three donor populations made equal or random genetic contributions to shoreline- and tributary-spawning populations in Frazer Lake.

Materials and methods

Study site and historical perspective

Frazer Lake (57°15′N, 154°8′W) is located on the southwest end of Kodiak Island, Alaska (Fig. 1), within the boundaries of the Kodiak National Wildlife Refuge. The lake is approximately 14 km long and 1.6 km wide and has a surface area of 16.6 km^2 and maximum and mean depths of 59 and 32.2 m, respectively (Russell 1972; Kyle et al. 1988). Water temperatures range from about 6 to 14°C during the spring and summer months, with the peak in mid- to late August (Eaton 1968). The lake outlet (Dog Salmon River) flows southwest about 14 km into Olga Bay.

Post-Pleistocene colonization of Frazer Lake by anadromous salmonids was precluded historically by a 10-m-high waterfall about 0.8 km downstream of the lake outlet. Resident rainbow trout (*Oncorhynchus mykiss*), Dolly Varden (*Salvelinus malma*), threespine stickleback (*Gasterosteus aculeatus*), and coastrange sculpin (*Cottus aleuticus*) were the only fish species observed in the lake during historic surveys; pink (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*) were the only salmon species present in the Dog Salmon River below the falls prior to sockeye introduction (Blackett 1979). A fishpass was installed at the falls in 1962 (see Blackett 1979) to allow sockeye salmon access to Frazer Lake and to enumerate returning adults. A second fishpass was installed in 1979 to aid growing numbers of returning adults (Kyle et al. 1988).

Sockeye salmon were first introduced into Frazer Lake in 1951 after limnological evaluations indicated suitable spawning and nursery conditions for this species. Introductions continued through 1971 (see Blackett 1979). Three separate donor populations of Alaskan sockeye salmon, each characterized by different life history attributes, were introduced: (*i*) a late-run lake shoreline

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Table 1. Summary of sockeye salmon donor plants (by life stage), donor sources, and resulting sockeye escapements to Frazer Lake, Alaska, 1951 to modern time.

Year	Number of donors and life stage			Donor source	Areas planted in Frazer Lake	Annual escapement[a]
	Adults	Fry	Eggs			
1951			200 000	D1	Stumble Creek	
1952			313 000	D1	Linda Creek	
1953			1 092 000	D1	Pinnell, Westside, Linda, Midway creeks	
1954			541 000	D1	Linda Creek	
1955			320 000	D1	Linda, Stumble creeks	
1956			504 000	D2	Linda, Stumble creeks	6
1957						165
1958	42			D2	Midway Creek	71
1959						62
1960						440
1961	600	87 000		D2	Lake (adults, fry)	273
1962	1 839			D2	Lake	1 290
1963	9 500			D2	Lake	2 357
1964	1 800			D2	Lake	8 166
1965	4 000		830 000	D2	Lake (adults); tributaries (eggs)	5 074
1966	4 728	504 300	600 000	D2	Lake (adults, fry); Stumble Creek (eggs)	11 728
1967	7 334		1 190 000	D2	Lake (adults); Midway, Pinnell, Linda creeks (eggs)	14 500
1968	30	311 000	3 387 000	D2	Lake (adults, fry); Midway, Pinnell, Linda creeks (eggs)	16 708
1969	60			D2	Lake	
1969		599 760	1 963 000	D3	Lake (fry); Midway, Linda creeks (eggs)	13 981
1970		945 000		D2	Pinnell Creek	24 039
1971		527 000		D2	Pinnell Creek	55 356
1990s						~200 000

Note: Data from Eaton (1968), Gwartney (1969), Russell (1972), Blackett (1979), and Swanton (1992). Karluk Lake donors (D1) were late-run shoreline spawners, Red Lake donors (D2) were early-run inlet tributary spawners, and Ruth Lake donors (D3) were late-run lake outlet spawners.

[a]Prior to fishpass construction, returning adults were backpacked over a waterfall for release into Frazer Lake (1956–1961).

spawning population from Karluk Lake (57°22′N, 154°2′W) on Kodiak Island, (*ii*) an early-run inlet tributary spawning population from Red Lake (57°15′N, 154°17′W) on Kodiak Island, and (*iii*) a late-run lake outlet spawning population from Ruth Lake (57°34′N, 156°7′W) located in the Becharof Lake drainage of Bristol Bay (Fig. 1). These three source populations are referred to as D1, D2, and D3, respectively.

Sockeye salmon representing a variety of life history stages were released or transplanted repeatedly into several different locations within Frazer Lake over the introduction period (Table 1). The D1 donors consisted of fertilized eggs from adults spawning along the Karluk Lake shoreline just east of an area known as O'Malley Beach, the D2 donors consisted of eggs, fry, and adults from Connecticut Creek, an inlet tributary flowing into the northeast corner of Red Lake, and the D3 donors comprised eggs and cultured fry from adults trapped in the middle reaches of the river draining Ruth Lake (historical details about donor capture sites obtained from R. Blackett, P.O. Box 593, Kodiak, AK 99615, U.S.A, personal communication). Eggs were planted into mechanically prepared redds in Frazer Lake tributaries, whereas most fry and adults were released directly into the lake. These latter transplants often occurred near the mouth of Pinnell Creek (Fig. 2), usually from the pontoons of a fixed-wing floatplane. Cultured fry from D3 (1969 only) were released into northern areas of the lake from floating plastic bags. In the final two years of introduction (1970 and 1971), cultured fry from D2 were released upstream in Pinnell Creek from a helicopter. Thus, the origins and spawning locations of the ancestral donors are well known, and much detail is available on the allocation of specific source populations and life history stages to Frazer Lake habitats during their 20 years of introduction (see information sources provided in Table 1).

Colonization and establishment of naturally spawning populations in Frazer Lake progressed rapidly after sockeye salmon were introduced. Adults first returned to Frazer Lake in 1956 (N = 6), with postharvest annual escapements steadily increasing to thousands of potential spawners by the late 1960s (Table 1). Prior to construction of the first fishpass, returning adults were transported above the falls in backpacks (Blackett 1979). By the 1980s, mean annual escapements had increased to over 256 000 adults and peaked at nearly 486 000 fish in 1985 (Kyle et al. 1988). Contemporary escapements (1990s) have averaged about 200 000 adults annually, from a total run size (including harvest) of nearly 1 million fish in some years (Swanton 1992). Based on a 1964 survey, Frazer Lake tributaries (Stumble, Linda, and Pinnell creeks; Fig. 2) were among the first habitats colonized by sockeye salmon (Meehan et al. 1965). Spawning in shoreline areas was first documented in 1966 (247 spawners) with an increase through 1970 (Gwartney 1969; Russell 1972). Aerial surveys conducted in 1987 estimated several thousand sockeye in shoreline-spawning areas from mid- to late August through the last week of September (Barrett 1989). Thus, existing records for Frazer Lake provide valuable insights into colonization success.

The upstream migration and spawning times of the three donor populations (Blackett 1979; Gard et al. 1987) are within the ranges typical for sockeye salmon in south-central Alaska (Burger et al. 1995). Early-run inlet tributary sockeye return from about mid-

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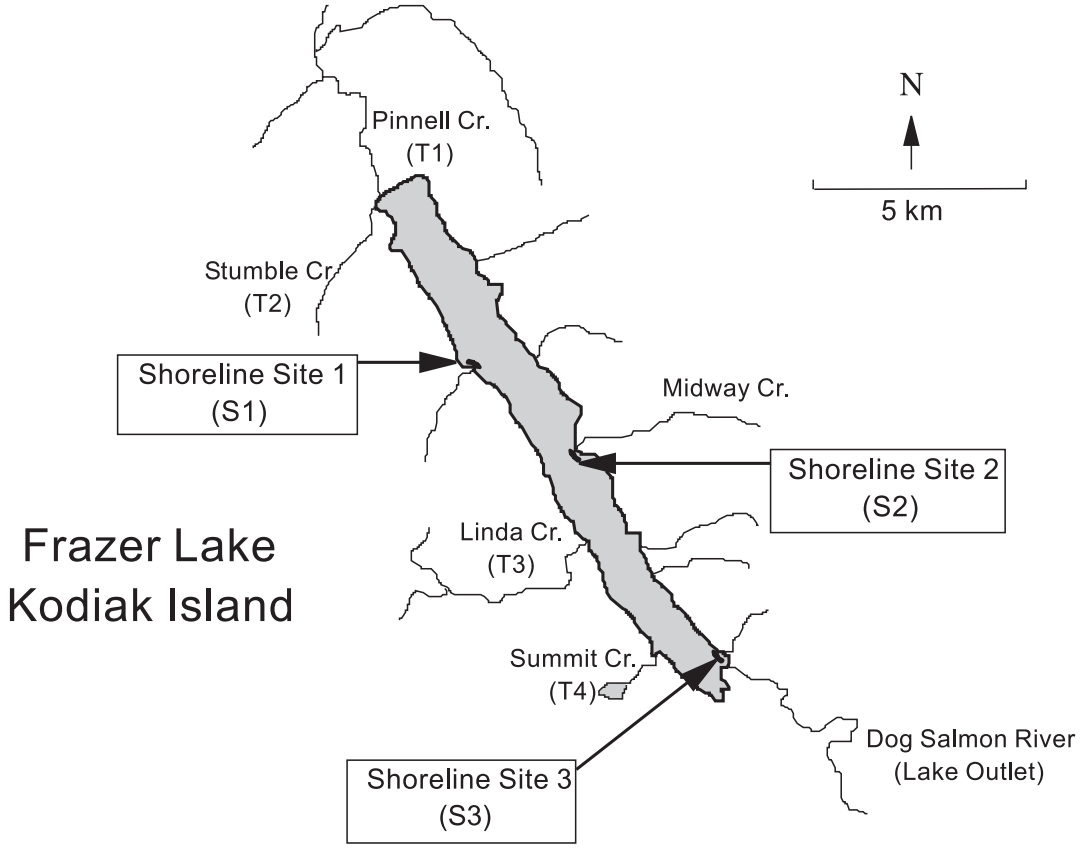
Fig. 2. Map of Frazer Lake drainage on Kodiak Island, Alaska, showing the inlet tributary streams (T1–T4) and shoreline spawning areas (S1–S3) from which sockeye salmon were sampled for genetic analyses.



June through July and spawn from mid-July through mid-August. In contrast, late-run shoreline and lake outlet sockeye return during August through early September and spawn from late August through late September. These life history differences provide a biological foundation for understanding colonization success, the population genetics of sockeye salmon, and the relative genetic contributions of the three donor populations to shoreline- and tributary-spawning aggregations in contemporary Frazer Lake.

Population samples

Tissue samples (portions of adipose fin with muscle) of adult sockeye salmon were obtained during late summer and fall of 1995 from each of the three donor populations and from fish spawning at three shoreline sites and four inlet tributary streams of Frazer Lake (Figs. 1 and 2). All fish were captured with beach seines and dip nets. Samples from D1, D2, and D3, respectively, were obtained on (*i*) 2 October (mostly spawned-out sockeye) at the shoreline location in Karluk Lake where adult fish were originally caught and spawned for the introduction program, (*ii*) 6 August (actively spawning and spawned-out fish) in the inlet tributary of Red Lake, and (*iii*) 18 August (unspawned ripe adults) in the outlet river of Ruth Lake. Sampling locations and times for the three donor populations were based on historic reports and personal communications with former employees of the Alaska Department of Fish and Game (ADFG). Each donor population had been historically large in size (thousands of spawners; R. Blackett, P.O. Box 593, Kodiak, AK 99615, U.S.A., personal communication), consistent with contemporary observations when donor populations were sampled for our study. We obtained samples of sockeye salmon in the Frazer Lake drainage between 4 and 8 August from three shoreline spawning sites (S1–S3) and four Frazer Lake inlet tributaries (T1–T4) (Fig. 2). The 4–8 August sampling period was chosen because aggregations of spawners are present simultaneously in all Frazer Lake habitats.

Sampling locations within Frazer Lake were based on spawner abundances documented in ADFG surveys. Fish sampled at shoreline sites were sexually mature, unspawned adults. Sampling in tributaries was conducted >30 m upstream of Frazer Lake. Many of the sockeye salmon in tributaries were spawned-out adults guarding redds, but actively spawning and dead fish were also observed. Only small numbers of spawners (<20 fish) were observed in other areas of Frazer Lake (i.e., in a few small tributaries) and were not sampled. These latter observations were consistent with those of Barrett (1989) and supported the information from ADFG that the seven sample sites (S1–S3 and T1–T4) represented the major spawning locations of sockeye salmon in the Frazer Lake system. We did not sample fish in the outlet of Frazer Lake (above the adult weir and fishpass) because a viable, self-sustaining population of sockeye salmon never became established there.

Tissue samples were initially frozen at –20°C and subsequently frozen at –70°C. DNA was extracted from a random subsample of 50 individuals from each of the three donor populations and from each of the seven Frazer Lake spawning aggregations that we sampled in the field. DNA was extracted using standard proteinase K and phenol–chloroform extraction techniques followed by ethanol precipitation. DNA concentrations were determined using fluorimetry; aliquoted stocks of 50 ng·mL^{-1} were made for all individuals.

nDNA (microsatellite) analysis

Six microsatellite loci were used for analysis: *One*μ1, *One*μ8, *One*μ11, *One*μ13, *One*μ14, and *One*μ18 (for methods and details, see Scribner et al. 1996). All polymerase chain reactions (PCR)

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were 35 cycles in duration (94°C denaturation for 1 min, annealing for 1 min at locus-specific temperatures, and extension at 72°C for 1 min) and were conducted in 25-μL volumes using approximately 100 ng of DNA, buffer (10 mM Tris–HCl, pH 8.3, 1.5 mM $MgCl_2$, 50 mM KCl, 0.01% gelatin, 0.01% NP-40 (BioRad), and 0.01% Triton-X 100 (Sigma)), and 0.25 units of *Taq* polymerase (Perkin Elmer). Primer, dNTP concentrations, and annealing temperatures for each locus were 33 nM primer and 20 μM dNTP at 60°C (*One*μ8), 0.40 μM primer and 160 μM dNTP at 54°C (*One*μ18), 0.40 mM primer and 160 mM dNTP at 52°C (*One*μ13; also included 2.5% DMSO and $MgCl_2$ at 2.0 mM), and 0.40 μM primer and 160 μM dNTP at 60°C (*One*μ11). Loci *One*μ1 and *One*μ14 were coamplified using conditions specified by Olsen et al. (1996). For these loci, the annealing temperature was 58°C, dNTP concentration was 200 μM, *One*μ1 primers were at 0.13 μM, and *One*μ14 primers were at 0.19 μM.

mtDNA analysis

Two regions of the mitochondrial genome (cytochrome *b* and ND 5/6) were surveyed for genetic variation using restriction endonuclease digestion of PCR products. Conserved oligonucleotide primers LGL 765 and LGL 287 (cytochrome *b*; see Bickham et al. 1995) and LGL 763 and LGL 764 (ND 5/6; see Cronin et al. 1993) amplified approximately 1200 and 2500 base pair segments of the cytochrome *b* and ND 5/6 regions, respectively. PCR reactions were conducted in 50-μL volumes using 100–500 ng of genomic DNA, buffer (10 mM Tris–HCl, pH 8.5, 50 mM KCl, 1 μg bovine serum albumin·μL^{-1}), 1.5 mM $MgCl_2$, 0.2 mM dNTP, 0.1 μM primer, and 1.25–2.5 units of *Taq* polymerase. Amplification was initiated with a single denaturation phase of 95°C for 4 min and progressed to 32 cycles of 94°C for 45 s, 50°C for 30 s, and 70°C for 2.5 min. Amplification products for the cytochrome *b* region were digested with five restriction enzymes (*Bfa*I, *Bsa*JI, *Bst*EI, *Dpn*II, and *Rsa*I) under conditions specified by the manufacturer (New England Biolabs). PCR products from the ND 5/6 region were digested with two restriction enzymes (*Apa*I and *Taq*I). The digests were run on 2% agarose gels with TBE buffer (Sambrook et al. 1989), stained with ethidium bromide, and photographed under ultraviolet light (312 nm). mtDNA haplotypes were defined on the basis of the composite presence or absence of restriction sites across all restriction enzymes (see Appendix A).

Statistical analysis

Microsatellite allele and mtDNA haplotype frequencies were calculated for each of the three donor populations and for each of the seven Frazer Lake spawning aggregations (hereafter referred to as "populations"). Deviations of genotypic proportions from Hardy–Weinberg expectations at the microsatellite loci were tested for statistical significance ($\alpha = 0.05$) with Fisher's exact test using GENEPOP (Raymond and Rousset 1995). Significance of multiple *P* values was adjusted for multiple testing (i.e., number of loci) using a Bonferoni correction (Manly 1985). Estimates of expected heterozygosity (under Hardy–Weinberg), direct-count heterozygosity, and number of alleles per locus were calculated using the program BIOSYS (Swofford and Selander 1981).

Estimated *F* statistics (Weir and Cockerham 1984) were used to partition allele frequency variation within and among populations. Analyses for the six microsatellite loci were conducted using FSTAT (Goudet 1995). An analogous measure of interpopulation variation based on correlations in allele size (Rho_{ST} ; Rousset 1996) was estimated as described by Michalakis and Excoffier (1996) using GENEPOP. The *F* statistics and Rho_{ST} were subsequently estimated for the Frazer Lake populations and the three donor populations. A complementary analysis of mtDNA variation was also conducted using an analysis of molecular variation (AMOVA) in which we calculated a haploid analog of F_{ST} (Φ_{ST}) applicable to DNA sequence data, based solely on haplotype frequencies independent of sequence relationship (Excoffier et al. 1992).

Genetic similarities among populations were further quantified based on genetic distances. The chord metric of Cavalli-Sforza and Edwards (1967) was used to calculate genetic distances between populations based on the six microsatellite loci. This metric has been described as providing robust intraspecific topologies based on microsatellite allele frequencies (Takezaki and Nei 1996). Given the short period of time (<50 years) between the initial stocking and our sampling of Frazer Lake populations, it was deemed unnecessary to use other distance metrics that have been advocated for microsatellite data based on allelic length variation. Processes most germane to this presentation are migration and genetic drift and not the accumulation of mutations postdating the introduction. Pairwise population estimates of the variance in mtDNA haplotype frequencies (θ) were used to estimate genetic distance for mtDNA ($D = -\ln(1 - \theta)$) as described by Reynolds et al. (1983) (also see eq. 5.12 in Weir (1996) and associated corrigendum). Matrices of pairwise genetic distances between samples were used as input for principal coordinates analyses (PCA) in order to provide a graphic representation of genetic distances in two dimensions. Eigenvector components were scaled such that their sums of squares equaled the corresponding eigenvalue (i.e., variance associated with the PC axis). The analysis followed the algorithm of Everitt (1978) for a distance matrix.

Mantel analyses (Smouse et al. 1986) were conducted on the seven contemporary Frazer Lake populations to determine if pairwise genetic distances among Frazer Lake populations are correlated with (*i*) straight-line geographic distances among spawning locales in Frazer Lake or (*ii*) spawning habitat types among sampled populations. This matrix regression technique tests for significant relationships between a dependent variable (interpopulation genetic distance) and each of several explanatory independent variables (geographic distance between spawning locations or spawning habitat types). The significance of observed matrix correlations (*r*) was determined using the random permutation tests described in Smouse et al. (1986).

The proportional genetic contributions (i.e., admixture proportions) of each of the three donor populations to each of the sockeye salmon populations in Frazer Lake were estimated by least squares regression based on the microsatellite allele frequency data (see Campton 1987). For each allele at each locus, the basic linear equation was

$$F_{ij} = b_1 D_{ij1} + b_2 D_{ij2} + b_3 D_{ij3} + e_{ij}$$

where F_{ij} is the frequency of the *j*th allele at the *i*th locus in one of the Frazer Lake populations (samples), D_{ijk} is the frequency of the same allele in the *k*th donor population ($k = 1$, 2, or 3), b_1, b_2, and b_3 are the regression coefficients to be estimated and are the proportional genetic contributions of D1, D2, and D3, respectively, to a Frazer Lake population (sample), and e_{ij} is the residual error term, the sum of squares of which is minimized. A total of 50 microsatellite alleles were observed (see Results); thus, 50 linear equations were used to estimate b_1, b_2, and b_3 for each of the seven Frazer Lake populations. The three regression coefficients were estimated by PROC REG of the SAS statistical package (SAS Institute Inc., P.O. Box 8000, Cary, NC 27511-8000, U.S.A.) with a no-intercept model (see above) and the restriction that $b_1 + b_2 + b_3 = 1.0$. The six loci were weighted equally in the regression analyses by using the WEIGHT statement of SAS to weight equations for alleles at the *i*th locus by $50/k$, where *k* equals the number of alleles at that locus. Without this procedure, loci with more alleles would have been given more weight. The regression analyses were performed with and without the arcsine square root transformation applied to all allele frequencies. Analysis of the untransformed allele frequencies yielded higher coefficients of determination (R^2)

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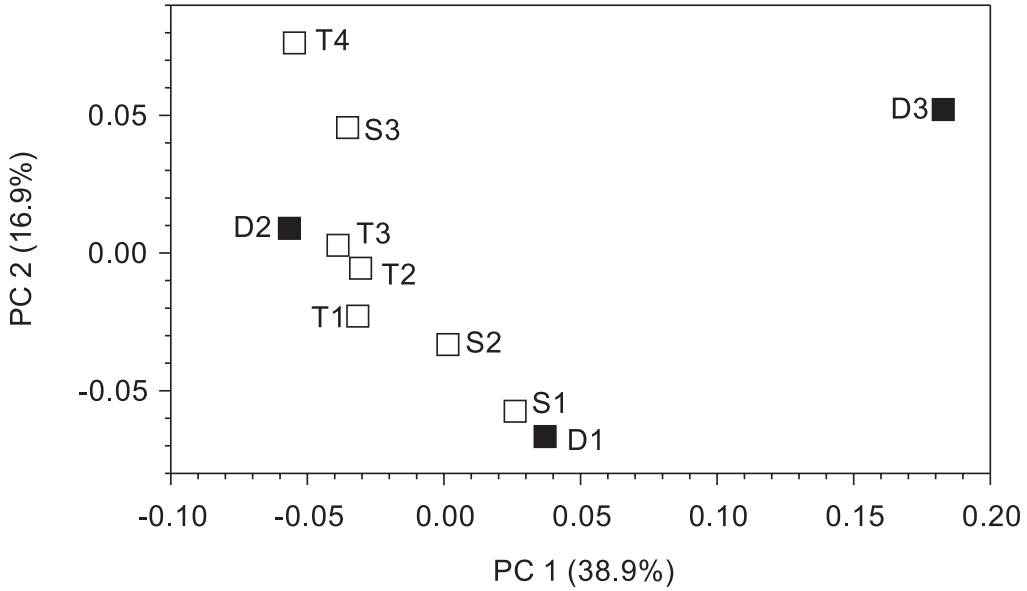
Table 2. Estimates of Wright's *F* statistics (*F*, *f*, θ_{ST}; Weir and Cockerham 1984; Goudet 1995), Φ_{ST} (an F_{ST} analog; Excoffier et al. 1992), and Rho_{ST} (Michalakis and Excoffier 1996) from genetic analyses of six microsatellite loci and mtDNA of sockeye salmon from three donor populations and from seven populations spawning within Frazer Lake, Alaska, 1995.

	Measure of interpopulation genetic variation							
	Among donor populations				Among Frazer Lake populations			
Locus	*F*	*f*	θ_{ST}	Rho_{ST}	*F*	*f*	θ_{ST}	Rho_{ST}
*One*μ18	0.057	0.017	0.041*	0.066*	0.009	0.006	0.003	–0.001
*One*μ11	0.048	–0.032	0.078*	–0.005	–0.006	–0.016	0.009*	–0.002
*One*μ8	0.118	0.081	0.040*	0.005	0.025	0.024	0.003	–0.002
*One*μ1	0.141	0.113	0.032*	0.030*	0.039	0.022	0.018*	0.014*
*One*μ14	0.105	0.092	0.015*	0.028*	–0.016	–0.013	0.003	0.004
*One*μ13	0.039	–0.013	0.052*	0.060*	–0.029	–0.033	0.003	0.005
Mean	0.081	0.039	0.044*	0.033*	0.002	–0.002	0.004*	0.000
mtDNA (θ_{ST})			0.062*				0.031*	

Note: *F*, *f*, and θ_{ST} are estimates of F_{IT}, F_{IS}, and F_{ST}, respectively. *$P < 0.05$.

Fig. 3. PCA plot of Frazer Lake sockeye salmon populations and their putative donor populations on two PC axes (Everitt 1978) based on allele frequencies at six microsatellite loci (Appendix A) and the chord genetic distance of Cavalli-Sforza and Edwards (1967) (Appendix B). Donor populations D1, D2, and D3 are indicated by solid squares and represent shoreline-, inlet tributary, and outlet-spawning life history types, respectively. Tributary- (T1–T4) and shoreline-spawning (S1–S4) populations within Frazer Lake are indicated by open squares.



than the analysis of transformed allele frequencies for all seven Frazer Lake populations; consequently, only results based on the untransformed allele frequencies are presented. Also, pooling minor alleles within samples (frequency <0.05) or setting sample allele frequencies of zero (0.00) to 0.01 had little effect on the estimated admixture proportions. Because each donor population consisted of thousands of spawners each year, our analysis assumes that allele frequencies for donor populations have remained constant since introductions into Frazer Lake commenced. This analysis also assumes that allele frequencies for the donor populations have been estimated without error (i.e., fixed parameters).

Results

Allele and haplotype frequencies differed significantly ($P < 0.05$) among the three donor populations and among the seven Frazer Lake populations, with greater genetic variation among the former (Table 2; Appendix A). Mean interpopulation variance in allele frequencies at the microsatellite loci (assessed as mean θ_{ST}) was approximately 10 times greater among the donor populations than among the Frazer Lake populations (0.044 versus 0.004, respectively) (Table 2). Estimates of interpopulation variance based on mtDNA (Φ_{ST}) for the donor (0.062) and Frazer Lake populations (0.031) were more similar than the corresponding statistics based on the microsatellite loci (θ_{ST}). For the Frazer Lake populations, Φ_{ST} based on mtDNA substantially exceeded the corresponding mean θ_{ST} based on the microsatellite loci, whereas values of the two statistics were similar for the donor populations. Genotypic proportions at the microsatellite loci did not deviate significantly from Hardy–Weinberg expectations except at one locus in one sample (*One*μ14, Ruth Lake outlet donor; $P < 0.05$).

Microsatellite allele frequencies and associated genetic distances for the Frazer Lake populations were generally in-

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Fig. 4. Same as Fig. 3 except that an outlier population (D3) was removed from the analysis and new principle coordinates were derived for the remaining nine populations.

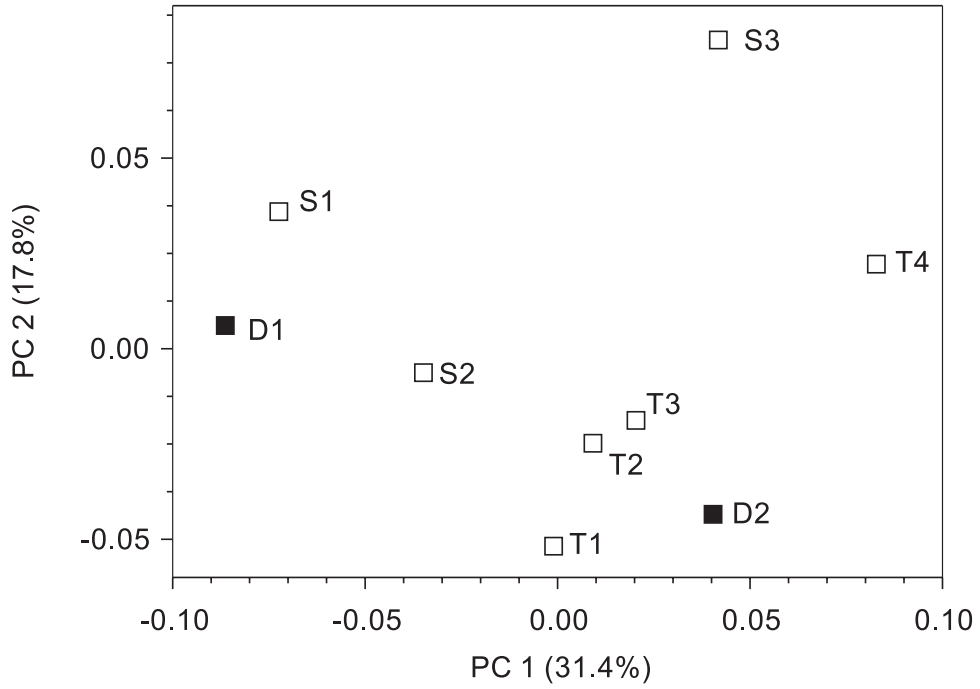
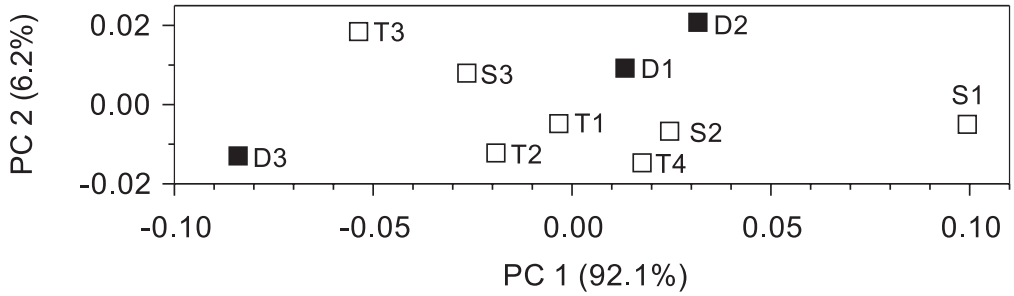


Fig. 5. PCA plot of Frazer Lake and putative donor populations based on mtDNA haplotype frequencies and the genetic distance measure of Reynolds et al. (1983) (Appendix B). Notations are the same as those in Fig. 3.



termediate to those distinguishing the Karluk (D1) and Red Lake (D2) donor populations (Appendices A and B; Fig. 3). Based on these genetic distances, all four of the Frazer Lake tributary populations were most similar to the Red Lake tributary donor population (D2), whereas two of the Frazer Lake shoreline populations (S1 and S2) were most similar to the Karluk Lake shoreline donor (D1). The Ruth Lake outlet population (D3) was clearly an outlier, quite distinct from the other sampled populations (mean D = 0.232, range 0.209–0.254) (Appendix B). Also, the S3 and T4 Frazer Lake populations (Fig. 2) were slight outliers in the PCA plot relative to the other Frazer Lake populations and the D1 and D2 donors (Fig. 4).

Genetic distances among the donor and Frazer Lake populations based on the mtDNA data were not consistent with genetic distances obtained from the microsatellite data (Appendix B; Fig. 5). In contrast with the microsatellite DNA data, differences in mtDNA haplotype frequencies among the Frazer Lake populations were substantially greater than the corresponding difference between the D1 and D2 donor populations. Haplotype frequencies for the Ruth Lake outlet population (D3) tended to be skewed towards the end of the observed range of haplotype frequencies, a result consistent with this donor population appearing to be a genetic outlier based on the microsatellite DNA analysis.

Genetic distances among the Frazer Lake populations based on microsatellite allele frequencies were correlated with spawning habitat type (tributary versus shoreline; Mantel r = –0.337, P = 0.013) but not with their straight-line (minimal) geographic distances (r = –0.181, P = 0.220). In contrast, the mtDNA genetic distances exhibited no consistent trend in population genetic similarity among Frazer Lake populations relative to spawning habitat type or geographic distance. Thus, populations in the Frazer Lake system, while differentiated with respect to mtDNA haplotype frequencies, were not spatially structured by spawning habitat or geographic proximity based on those frequencies.

The Karluk Lake shoreline donor population (D1) made the largest estimated genetic contribution to two (of three) shoreline populations in Frazer Lake, whereas the Red Lake tributary donor (D2) made the largest contribution to the four tributary populations (Table 3). The proportional ge-

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Table 3. Least squares estimates ± SE of the proportional genetic contribution of three donor populations (D1, Karluk Lake; D2, Red Lake; D3, Ruth Lake) to each of seven populations of sockeye salmon (S1–S3, shoreline spawners; tributary spawners: T1, Pinnell Creek; T2, Stumble Creek; T3, Linda Creek; T4, Summit Creek) in Frazer Lake, Alaska.

	Estimated genetic contribution to Frazer Lake populations			
	D1	D2	D3	R^2
S1	0.552±0.046***	0.418±0.039***	0.030+0.032	0.995
S2	0.483±0.054***	0.398±0.046***	0.119±0.038**	0.994
S3	0.119±0.113	0.502±0.097***	0.379±0.080***	0.970
T1	0.273±0.063***	0.751±0.054***	–0.024±0.045	0.992
T2	0.441±0.060***	0.591±0.051***	–0.031±0.042	0.993
T3	0.074±0.084	0.856±0.072***	0.070±0.060	0.986
T4	0.189±0.095	0.709±0.082***	0.102±0.068	0.980

Note: R^2 is the coefficient of determination for the multiple regression sum of squares. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

netic contribution of the Red Lake donor population to the four tributary populations in Frazer Lake ranged from 0.591 ± 0.051 (T2) to 0.856 ± 0.072 (T3). However, the shoreline donor population from Karluk Lake appears to have also contributed significantly ($P < 0.001$) to two of those Frazer Lake tributary populations (T1 and T2). Similarly, the Red Lake tributary donor population appears to have made significant genetic contributions ($P < 0.001$) to all three shoreline populations in Frazer Lake. The Ruth Lake outlet donor population (D3) made no detectable genetic contribution to the Frazer Lake tributary populations but may have made a significant contribution ($b_3 = 0.379 \pm 0.080$; $P < 0.001$) to shoreline population S3 nearest the lake's outlet (Fig. 2). These estimated genetic contributions (Table 3) are very consistent with the relative positions of the populations in the PCA biplots (Figs. 3 and 4) and their underlying genetic distances (Appendix B). In summary, six of the seven Frazer Lake populations appear to have been derived mostly from donor populations of corresponding life history and spawning-habitat types, but five Frazer Lake populations (S1–S3, T1, and T2) appear to have been genetically influenced by more than one donor.

Discussion

Life history diversity and natural colonization

Sockeye salmon exhibit a remarkable diversity of freshwater life history variation, particularly with respect to temporal and spatial aspects of migration, spawning, and rearing behaviors (reviewed by Burgner 1991). These adaptations appear to have facilitated natural colonization in an array of environments, factors that must be considered in any reintroduction or restoration effort. Several ecological forms of sockeye salmon have evolved: nonanadromous kokanee populations, believed to have arisen polyphyletically from anadromous forms in many lake–river systems (Wood and Foote 1996), lake "residual sockeye" that are the nonmigratory offspring of anadromous parents (Burgner 1991), and various anadromous populations that have colonized a large number of drainages throughout the North Pacific Rim. Although some anadromous populations exhibit "sea–river-type" characteristics and spawn in drainages devoid of lakes (Eiler et al. 1992), most are "lake-adapted" forms that reproduce in watersheds with lacustrine nurseries. The lakes confer survival advantages to juveniles (Burgner 1991; Wood 1995). Even within a single lake–river system, considerable temporal and spatial variation in spawning and rearing behavior is present among anadromous forms (Brannon 1987; Burger et al. 1995). Thus, a wide range of habitats has led to the evolution of a complex pattern of life history adaptations associated with migration timing, reproduction, fry emergence, and rheotactic orientation of juveniles not seen in other species of Pacific salmon (Burgner 1991).

Natural colonization of lake–river systems by sockeye salmon can be quite rapid following glacial retreats (Milner and Bailey 1989); however, the mechanism by which colonization occurs is not well understood. Wood (1995) has suggested that sea–river-type sockeye salmon are the principal colonizers of new habitats following glacial retreats. These fish are known to inhabit glacially influenced rivers, and genetic data for a number of populations suggest that sea–river forms stray more than lake-adapted populations (Wood et al. 1994; Gustafson and Winans 1999). The perplexity is to understand how ecological and genetic divergence proceeds, once initial colonization has occurred via straying. Does the initial colonizing population subsequently diverge into locally adapted subpopulations of tributary-, shoreline-, and outlet-spawning fish, or does colonization proceed via multiple, independent straying events? Although such questions are not immediately answerable, habitat variability and complexity are thought to be the templates, or driving mechanisms, that yield diverse, locally adapted populations of Pacific salmon. As a glacier begins to retreat from a large lake, the lake's lateral tributaries may be the first habitats to warm and become colonized, with shoreline and outlet rivers colonized later, as the glacier completes its recession from the lake proper (Burger et al. 1997). To the extent that such a process occurs, the lateral tributaries could provide the initial colonization habitat for sea–river-type sockeye, a form known to stray, and one already adapted for riverine-like conditions (Wood 1995). Thus, thermally diverse environments that develop following glacial recessions may promote natural selection, genetic divergence, and local adaptation of sockeye salmon (Burger et al. 1997). The introduction of three distinct life history forms of sockeye salmon, presumably preadapted to such conditions in Frazer Lake, may have been an important factor contributing to their colonization success.

Genetic structure of Frazer Lake populations

We reject the null hypothesis of a single, panmictic population of sockeye salmon in Fraser Lake based on both the microsatellite and mtDNA data. Interpopulation divergence of mtDNA haplotype frequencies in the Frazer Lake system was nearly as large as the variation among the donor populations. These results are consistent with very little gene flow among Frazer Lake populations, including geographically adjacent populations. Significant differences in microsatellite allele frequencies further support this interpretation. The microsatellite data also provide strong support that Karluk Lake shoreline (D1) and Red Lake tributary (D2) do-

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nors were the principal contributors to existing shoreline and tributary spawners, respectively, in Frazer Lake. With one possible exception (S3), the Ruth Lake outlet donor (D3) appears to have made little or no genetic contribution to contemporary Frazer Lake populations. These conclusions are supported by our estimates of admixture proportions and by Mantel analyses. These latter correlations statistically support the argument, based on genetic distances, of greater genetic similarity among shoreline-spawning populations and among tributary-spawning populations than among geographically adjacent populations. Indeed, the Mantel analysis allowed us to reject the alternative hypothesis that geographic proximity or distance is the primary determinant of the observed genetic distances. Such a result is remarkable given the recent ancestry of these populations in a system as small as Frazer Lake. The most parsimonious explanation for this relationship is one involving common ancestral origins among the shoreline spawners and among the tributary spawners in Frazer Lake.

Genetic distances and relationships derived from the mtDNA data were not consistent with those obtained from the microsatellite data. Whereas the microsatellite data yielded a predictable pattern of population structure and donor relationships based on life histories and habitat types, genetic distances among populations based on mtDNA appeared to be random. The two sets of markers thus yielded fundamentally different results with respect to the relative genetic distances among the sampled populations.

We suggest that significant female founder effects and subsequent genetic drift of mtDNA haplotype frequencies within Frazer Lake may have been the principal causes of the inconsistency between the microsatellite and mtDNA data. We assume that both mtDNA and microsatellite alleles are effectively neutral markers, particularly over the time span since colonization of Frazer Lake began. Over such short periods of time, mutational rate differences between the two types of markers can be excluded as the source of the inconsistency. However, mtDNA markers are substantially more sensitive to "bottlenecks" and founder effects because of a fourfold lower effective population size (N_e) compared with nDNA markers (Birky et al. 1983). The nearly 10-fold higher Φ_{ST} for mtDNA versus the mean θ_{ST} at the six microsatellite loci (i.e., for the Frazer Lake populations) is consistent with expectations for populations undergoing founder effects and genetic drift due to dynamic changes in abundance and low effective population sizes. Similar values of θ_{ST} and Φ_{ST} among the three donor populations are consistent with expectations for long-standing populations in migration–drift equilibrium. We thus believe that the microsatellite data provide a much more accurate record of population ancestries in Frazer Lake than the mtDNA data. Estimates of admixture proportions and donor contributions were thus based strictly on the microsatellite data.

Estimating the proportional genetic contribution of two or more donor populations to a genetically admixed hybrid population is a fundamental problem in population genetics (Chakraborty 1986; Long 1991). Multilocus methods based on least squares and maximum likelihood have been developed, but all of these methods are limited by three underlying assumptions: (1) allele frequencies for the donor populations are estimated without error and have not changed temporally since the initial hybridization event (no selection, migration, mutation, or drift), (2) allele frequencies for the hybrid population are temporally stable and thus reflect the proportional genetic contributions of the donor populations, and (3) all potential donor populations are known and are included in estimation equations. Violation of the first two assumptions primarily affects the standard errors of estimates, whereas violation of the third assumption primarily affects the point estimates themselves. Despite these limitations, the various least squares and maximum likelihood methodologies generally yield similar results when applied to a particular data set (Chakraborty 1986).

Our estimates of admixture proportions for Frazer Lake populations must therefore be interpreted in the context of two potential sources of error. First, our standard errors of the estimates are undoubtedly less than their true values because of an unknown amount of genetic and statistical sampling error (assumptions 1 and 2 of the preceding paragraph). Despite these uncertainties, an arbitrary doubling or tripling of our standard errors still yields estimates that support detectable genetic contributions by both Karluk Lake shoreline donors (D1) and Red Lake tributary donors (D2) to (*i*) two of the four tributary populations (T1 and T2) and (*ii*) two of the three shoreline populations (S1 and S2) in Frazer Lake, with contributions skewed towards the donor population of the same life history type. These estimates thus provide clear genetic signals regarding the population dynamics of the colonization process. Second, we have assumed that all potential donor populations are known and were accurately included during our field sampling based on the well-documented stocking history of sockeye salmon in Frazer Lake. However, we cannot exclude the possibility that one or more unknown donor populations may have contributed genetically to Frazer Lake populations via natural straying. As described previously, natural straying is a life history strategy of sockeye salmon that allows rapid colonization of newly deglaciated lakes and watersheds (Burgner 1991; Wood 1995). The presence of several alleles in one or more Frazer Lake populations (e.g., *One*μ11*138 in S3 and T4), coupled with their absence in samples from known donor populations, is consistent with a possible straying influence. Additional sampling and study are thus desirable to test this latter hypothesis.

Ecological considerations and local adaptation

The life history characteristics of the sockeye salmon donor populations appear to have provided the fundamental biological capabilities for survival and successful colonization of ecologically distinct spawning habitats in Frazer Lake. In a relatively small system such as Frazer Lake, historic straying over time could be expected to homogenize gene frequencies. For example, transplanted salmonids are known to stray more than indigenous populations (Quinn 1993). Nevertheless, distinct populations of shoreline- and tributary-spawning sockeye salmon appear to exist in Frazer Lake despite their relatively recent introduction. Although paired adults were observed in the lake's outlet in the late 1970s (Blackett 1979), colonization did not occur in this area, possibly because stocking with Ruth Lake outlet donors occurred in only one year and because minimal spawning

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habitat exists between the lake's outlet and the fishpass. In addition, during the mid- to late 1980s, the fishpass was deliberately closed in mid-August to prevent overescapement into the lake, and this closure may have precluded development of late-run outlet spawners. In prior years, the fishpass remained open through August and sometimes into September, thus providing adults access to diverse spawning habitats at times conducive to the development of early and late life history forms (Russell 1972; Blackett 1979). Frazer Lake habitats were thus available for colonization by discrete early and late seasonal runs of sockeye salmon for more than 30 years after the first transplant's occurred in the drainage.

Establishment of distinct early- and late-run spawners in Frazer Lake (in its tributaries and shorelines, respectively) may have occurred quite early during the colonization process. Sockeye salmon colonized the lake's inlet tributaries first (by 1964) and then the shorelines (Meehan et al. 1965; Russell 1972). In 1987, Barrett (1989) found substantial numbers of shoreline spawners during the first apparent spawning survey conducted in late September at Frazer Lake. Consequently, shoreline spawning during late September was probably occurring in earlier years but was not observed. Monthly estimates of annual escapements of sockeye salmon into Frazer Lake during the late 1960s suggest bimodality in run timing with a large escapement peak from late June through early July and a second, sometimes smaller peak from late July through early August (Russell 1972). These data suggest that early and late runs of sockeye salmon (primarily reflecting tributary and shoreline spawners, respectively) were already developing in Frazer Lake by the late 1960s, with run and spawning times approximating those of early-run Red Lake tributary donors (Blackett 1979) and late-run Karluk Lake shoreline donors (Gard et al. 1987). Also, Frazer Lake appears to have provided the necessary range of thermal characteristics (Meehan et al. 1965) optimal for successful colonization by both early and late seasonal forms of Alaskan sockeye salmon (Burger et al. 1995, 1997).

Populations of sockeye salmon in Frazer Lake may not have yet reached a state of demographic or genetic equilibrium. Substantial changes in the relative abundance, spawning distribution, and age structure of sockeye salmon in Frazer Lake have occurred since the colonization process began (<10 generations). For example, in 1977 and 1978, nearly 84% of all sockeye salmon escaping to Frazer Lake spawned between 20 July and 20 August in a single inlet tributary, Pinnell Creek (Blackett 1979). In 1987, however, peak tributary spawning of sockeye occurred during the third week of August, whereas shoreline spawning occurred through late September (Barrett 1989). In addition, the number of shoreline spawners in 1987 was, for the first time, approximately twice the number of spawners observed in Pinnell Creek in earlier years. These observations indicate that the population dynamics of sockeye salmon in Frazer Lake have been in flux and that the number of shoreline spawners increased substantially during the 1980s. Moreover, the predominate age-class of adult sockeye salmon in Frazer Lake has fluctuated greatly over the past 30 years (Kyle et al. 1988; Barrett 1989; Swanton 1992). Chronological "pulses" by specific age-classes may represent donor-mediated founder effects, consistent with genetic observations based on mtDNA data, but may also reflect fluctuating ocean conditions and varying smolt-to-adult survivals. Consequently, sockeye salmon in Frazer Lake may still be in a formative stage of adaptive evolution.

Genetic analyses of sockeye salmon in other Alaskan drainages (Burger et al. 1995, 1997) indicate that genetic divergence within lakes is typically associated with variations in seasonal run timing and spawning behavior, not with geographic distance between spawning habitats within the drainage, results consistent with those reported here for Frazer Lake. Indeed, other investigators have found no clear geographic pattern in allozyme frequencies among sockeye salmon populations in different lakes despite a rather large sampling effort across the Pacific Northwest (Winans et al. 1996). Moreover, allele frequencies among distinctly different ecological forms within a lake appear to remain stable over time (Altukhov and Salmenkova 1991). Such results imply little within-lake straying among populations and implicate the nursery lake as a principal foundation for local adaptations, further supporting the coexistence of genetically diverged subpopulations within surprisingly small spatial scales (Wood 1995). Sockeye salmon home to lake-associated streams with a high level of precision, possibly because natal lake systems have more distinctive odors than isolated rivers and streams (Quinn 1985). The homing instinct thus provides an adaptive mechanism for fine-scale genetic structuring. The disjunct nature of genetic divergence among sockeye salmon populations may be associated with the mosaic of available spawning habitats and the apparent precise degree to which adults home to nursery lakes and natal streams (Winans et al. 1996).

Management implications

Numerous studies have addressed concerns about matching genetic characteristics of donor populations with those of recipient populations and environments. Investigators frequently mention the need for monitoring and evaluation of introduction and restoration programs (Krueger et al. 1981; Waples 1991), especially for hatchery supplementation of natural populations (Allendorf and Waples 1996). However, comparatively little attention has been focused on the importance of life history traits and other heritable phenotypic characteristics (Hard 1995). Collectively, our results suggest that successful introductions of anadromous salmonids are possible if the life history traits of the donor populations are compatible with habitat conditions in proposed areas of release. Geographically, life history variation of sockeye salmon may reflect adaptive convergence in similar habitats among different drainages and may provide biologists with the opportunity to more fully understand the colonization process and the origin of within-species variation. In other words, life history characteristics may be the key to successful colonization of newly opened habitats and not the absolute genetic or geographic distances between potential donor and recipient populations. The findings of this study imply that managers should first consider adaptive phenotypic traits in salmonid restoration or introduction programs. In the case of sockeye salmon, habitat-specific spawning requirements need to be considered, but other characteristics

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such as run and spawning times and juvenile behavioral patterns also need attention.

Given the need for careful consideration of life history requirements and reproductive adaptations, our results further suggest that genetic diversity can be maintained in salmon restoration programs. Contemporary spawners at Frazer Lake have retained high levels of within-population genetic variability and between-population phenotypic variability, commensurate with the donor populations from which they were established. In addition to colonizing new habitats quickly following glacial recessions, genetic divergence of ecologically different forms of sockeye salmon can occur within relatively short (<2000 years) geologic time frames (Burger et al. 1997). Apparently, the diverse habitats available at Frazer Lake enabled rapid colonization by sockeye salmon donor populations already adapted for such conditions. Further, and as seen in other portions of their native range, the homing fidelity of sockeye salmon coupled with habitat-related differences in run timing can impede gene flow significantly and thus reinforce local adaptations across microgeographical spatial scales.

In conclusion, our study provided a unique opportunity to compare genetic relationships among recently founded populations of sockeye salmon in Frazer Lake, Alaska, with those of three putative donor populations that were deliberately introduced into a lake initially devoid of this species and other anadromous salmonid fishes. Such comparisons are rare, particularly for situations where the time frames of colonization are well established and stocking histories are known. In most cases, donor sources and stocking intensities are not completely known (e.g., Hendry et al. 1996). In the case of Frazer Lake, accurate records were maintained that described in detail the origin and stocking intensity of the ancestral donors, the life history stages introduced, the areas in which the donors were released or transplanted, and the methods used to accomplish the introductions (Blackett 1979).

Keys to success of the Frazer Lake introduction program centered on repetitive transplants over many years, large numbers of donors, use of different ecological forms, and variation in the life history stages of the fish introduced. The use of multiple donor sources, each having ecological traits and life history characters compatible with different Frazer Lake habitats, may have been the most important factor leading to successful colonization. Nevertheless, concerns regarding the potential for outbreeding depression (Gharrett and Smoker 1991; Reisenbichler 1997) must also be considered in stocking programs, but such concerns may be outweighed by the need to provide a breadth of life history and genetic diversity to initiate new colonization or restore otherwise extirpated populations. Data from the Frazer Lake experience provide valuable insights that may guide future management decisions for restoring or recovering natural populations by focusing on life history traits important to reintroduction efforts.

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Appendix A. Proportions of alleles (six microsatellite loci and mtDNA composite haplotypes) from samples representing different life history forms of sockeye salmon: lake shoreline, inlet tributary, and lake outlet spawners.

Locus/allele	Shoreline				Tributary					Outlet
(or haplotype)	D1	S1	S2	S3	D2	T1	T2	T3	T4	D3
Oneμ18										
169	—	—	—	—	—	0.010	—	—	0.010	—
171	0.470	0.459	0.441	0.490	0.423	0.412	0.469	0.471	0.551	0.230
173	0.030	0.010	0.039	0.030	0.019	0.010	—	0.010	—	—
175	—	—	—	—	—	—	—	—	0.010	0.010
179	—	—	—	—	—	—	0.010	—	—	—
181	0.090	0.143	0.137	0.150	0.221	0.147	0.146	0.265	0.153	0.180
185	0.390	0.388	0.373	0.320	0.337	0.422	0.375	0.245	0.276	0.550
187	—	—	0.010	—	—	—	—	—	—	0.030
189	0.020	—	—	0.010	—	—	—	0.010	—	—
N	50	49	51	50	52	51	48	51	49	50
Oneμ11										
138	—	—	—	0.050	—	—	—	—	0.030	—
144	0.050	0.050	0.029	—	—	0.029	0.030	0.010	0.010	0.100
146	0.010	—	—	—	—	—	—	—	—	—
148	0.750	0.790	0.745	0.650	0.846	0.824	0.810	0.755	0.730	0.530
154	0.190	0.160	0.226	0.300	0.154	0.147	0.160	0.235	0.230	0.370
N	50	50	51	50	52	51	50	51	50	50
Oneμ8										
192	—	0.020	—	0.010	—	—	—	—	0.010	—
196	—	—	—	—	—	—	—	—	—	0.010
198	0.052	0.051	0.070	0.110	0.096	0.100	0.070	0.073	0.100	0.204
200	0.010	0.031	0.012	—	—	0.010	—	0.021	—	0.041
202	0.010	0.082	0.012	0.010	0.019	0.020	0.010	—	—	0.020
204	0.521	0.449	0.570	0.530	0.404	0.540	0.570	0.573	0.540	0.245
206	0.281	0.153	0.174	0.150	0.212	0.150	0.140	0.135	0.090	0.235
208	0.010	0.020	—	0.010	0.010	—	0.010	0.010	0.030	0.020
210	0.031	0.112	0.047	0.130	0.106	0.050	0.060	0.073	0.050	0.010
212	—	—	—	—	0.010	—	—	—	0.010	0.020
214	0.063	0.082	0.081	0.030	0.019	0.050	0.070	0.042	0.030	0.184
216	—	—	—	—	—	—	—	—	0.040	—
218	0.021	—	0.035	0.020	0.125	0.080	0.070	0.073	0.100	—
226	—	—	—	—	—	—	—	—	—	0.010
N	48	49	43	50	52	50	50	48	50	49
Oneμ1										
112	0.092	0.070	0.078	0.170	0.029	0.020	0.082	0.040	0.080	0.180
114	0.847	0.880	0.882	0.810	0.933	0.971	0.918	0.940	0.900	0.780
116	0.051	0.050	0.029	0.020	0.039	0.010	—	0.020	0.020	0.040
118	0.010	—	0.010	—	—	—	—	—	—	—
N	49	50	51	50	52	51	49	50	50	50

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Appendix A (*concluded*).

Locus/allele	Shoreline				Tributary					Outlet
(or haplotype)	D1	S1	S2	S3	D2	T1	T2	T3	T4	D3
*One*μ14										
131	—	0.010	—	—	—	—	—	—	—	—
133	0.010	—	—	—	—	—	—	—	—	0.070
135	0.021	0.041	0.069	0.070	0.039	0.069	0.030	0.100	0.080	0.110
139	0.010	0.010	0.029	—	—	0.010	—	0.020	—	—
141	0.031	—	—	—	—	—	—	—	—	0.010
143	—	0.010	—	—	—	—	—	—	—	—
145	0.813	0.776	0.726	0.710	0.817	0.735	0.740	0.740	0.680	0.700
147	0.042	0.010	0.029	0.010	0.010	0.029	0.020	0.020	0.060	0.010
149	0.073	0.133	0.147	0.210	0.135	0.157	0.190	0.110	0.180	0.060
151	—	—	—	—	—	—	—	—	—	0.010
153	—	0.010	—	—	—	—	0.020	0.010	—	0.010
155	—	—	—	—	—	—	—	—	—	0.020
N	48	49	51	50	52	51	50	50	50	50
*One*μ13										
160	0.490	0.398	0.402	0.280	0.279	0.333	0.350	0.270	0.310	0.380
162	0.100	0.082	0.039	0.060	0.019	0.049	0.070	0.060	0.030	0.030
164	—	—	—	—	0.010	0.010	0.010	—	—	—
168	0.400	0.520	0.559	0.660	0.683	0.608	0.570	0.670	0.660	0.560
170	—	—	—	—	0.010	—	—	—	—	—
172	0.010	—	—	—	—	—	—	—	—	0.030
N	50	49	51	50	52	51	50	50	50	50
Mean H_{DC}	0.464	0.471	0.486	0.493	0.425	0.443	0.472	0.410	0.519	0.536
Mean H_{HW}	0.480	0.484	0.480	0.510	0.433	0.437	0.452	0.451	0.476	0.568
mtDNA										
ABBBABA	0.563	0.765	0.667	0.431	0.612	0.529	0.500	0.381	0.660	0.396
AAAABAA	0.208	0.216	0.275	0.333	0.163	0.333	0.417	0.405	0.320	0.453
AAAABAB	0.063	—	0.039	—	0.061	0.078	0.063	0.024	—	0.038
AAABABA	—	—	—	0.020	—	—	—	—	—	0.019
AAABABB	0.021	—	—	—	—	—	—	—	—	—
AABABAA	0.021	0.020	—	0.098	—	0.020	0.021	0.024	—	0.019
AABBABA	—	—	—	—	0.041	—	—	0.071	—	0.019
ABAABAA	—	—	—	—	0.082	—	—	0.048	—	0.038
ABAABAB	—	—	—	—	—	—	—	—	—	0.019
ABABABA	0.104	—	0.020	0.118	0.020	0.039	—	0.024	—	—
ABBABAA	0.021	—	—	—	—	—	—	—	—	—
ABBBABB	—	—	—	—	—	—	—	—	0.020	—
BAAABAA	—	—	—	—	—	—	—	0.024	—	—
BBAABAA	—	—	—	—	0.020	—	—	—	—	—
N	48	51	51	51	49	51	48	42	50	53
Haplotype diversity	0.625	0.368	0.479	0.680	0.585	0.603	0.572	0.684	0.463	0.636

Note: Samples include three donor populations (D1, Karluk Lake; D2, Red Lake; D3, Ruth Lake) once used to introduce sockeye salmon into Frazer Lake, Alaska, and sockeye salmon spawning in Frazer Lake shoreline sites (S1–S3) and inlet tributaries (T1, Pinnell Creek; T2, Stumble Creek; T3, Linda Creek; T4, Summit Creek) during 1995. Allele designations for microsatellite loci are in base pairs. mtDNA composite haplotypes are individual restriction fragment length polymorphisms in the order *Bfa*I, *Bsa*JI, *Bst*EI, *Dpn*II, and *Rsa*I (cytochrome *b* region) and *Apa*I and *Taq*I (ND 5/6 region). *N* is the number of fish in each sample. H_{DC} and H_{HW} refer to direct-count and Hardy–Weinberg expected values of heterozygosity, respectively.

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Appendix B. Pairwise genetic distances between samples of sockeye salmon from three donor source lakes (D1, Karluk Lake; D2, Red Lake; D3, Ruth Lake), three populations spawning at shoreline sites (S1–S3), and four populations spawning in Frazer Lake, Alaska, tributaries (T1, Pinnell Creek; T2, Stumble Creek; T3, Linda Creek; T4, Summit Creek).

	Shoreline				Tributary					Outlet
	D1	S1	S2	S3	D2	T1	T2	T3	T4	D3
D1	—	0.0354	0.0014	–0.0128	–0.0032	–0.0026	0.0271	0.0431	0.0143	0.0765
S1	0.144	—	–0.0018	0.1101	0.0203	0.0566	0.0951	0.1507	0.0069	0.1808
S2	0.114	0.125	—	0.0470	0.0027	0.0027	0.0256	0.0681	–0.0153	0.0898
S3	0.173	0.158	0.136	—	0.0511	0.0022	0.0077	0.0005	0.0449	0.0193
D2	0.172	0.167	0.137	0.143	—	0.0175	0.0511	0.0664	0.0173	0.1099
T1	0.143	0.139	0.089	0.152	0.108	—	–0.0123	0.0077	0.0039	0.0223
T2	0.152	0.143	0.120	0.143	0.130	0.096	—	–0.0032	0.0171	–0.0017
T3	0.153	0.152	0.106	0.134	0.121	0.103	0.119	—	0.0591	–0.0125
T4	0.187	0.187	0.151	0.131	0.145	0.137	0.135	0.131	—	0.0731
D3	0.209	0.214	0.211	0.242	0.254	0.233	0.234	0.238	0.251	—

Note: Pairwise distances are based on six microsatellite nDNA loci and the Cavalli-Sforza and Edwards (1967) genetic chord distance (below the diagonal) and mtDNA haplotype frequencies and the metric $-\ln(1 - \theta)$ of Reynolds et al. (1983) (above the diagonal).

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